

# BIOLOGY AND TAXONOMY OF THE GENUS *NEMATOSCELIS* (CRUSTACEA, EUPHAUSIACEA)

K. GOPALAKRISHNAN<sup>1</sup>

## ABSTRACT

The seven species of *Nematoscelis*, *N. difficilis*, *N. megalops*, *N. gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, and *N. lobata*, are described in a comparative manner, and keys for their identifications are provided. The key to the larvae is based on structural differences in the carapace and rostrum of furcilia stages, whereas the key to adults is mostly based on diagnostic features of the first thoracic leg (maxilliped) and a male secondary sexual structure, the petasma. *Nematoscelis gracilis* is represented by two distinct forms; they are considered ecophenotypes, since their patterns of geographical distribution appear correlated with differences in environmental characteristics, particularly the distribution of dissolved oxygen in the water column. Diagnostic features of these forms are pointed out. The antennule and carapace are sexually dimorphic in adults of all *Nematoscelis*. Abdominal photophores in the males show species-specific patterns of enlargement.

The genus *Nematoscelis* consists of seven species. It was described by G. O. Sars (1883, 1885) as consisting of *N. megalops*, *N. tenella*, *N. microps*, and *N. rostrata*. Hansen synonymized *N. rostrata* with *N. microps* and added four species: *N. gracilis* and *N. atlantica* in 1910, *N. difficilis* in 1911, and *N. lobata* in 1916. *Nematoscelis lobata* was not found by subsequent workers but the other species were discussed by Ruud (1936), Boden (1954), Boden et al. (1955) and Mauchline and Fisher (1969). Taxonomically *Nematoscelis* has been a difficult genus.

Like other species of euphausiids, *Nematoscelis* species have been identified mainly on the basis of differences in the male copulatory organ, the petasma. Since the petasma is an adult character, it has been difficult to identify immature specimens and mature females. Characters such as the shape of the eyes and structure of the second thoracic leg have been used to discriminate species. Einarsson (1942) showed structural differences in spermathecae (thelyca) of females, but such differences appear slight and are difficult to examine. Mauchline and Fisher (1969) pointed out difficulties encountered in the identification of species of this genus. In the present study an attempt is made to point out the diagnostic value of the first thoracic leg (maxilliped) in discriminating all species of *Nematoscelis*. This appendage

usually remains attached to the animal caught by nets (as compared with the elongate second leg which is usually lost). It can be used as a diagnostic character in both sexes. The structural differences among the petasmae are also reexamined. The morphology of individual species will not be given separately, but species differences will be pointed out in a comparative manner. Since all species of this genus are sexually dimorphic, it is necessary to describe both sexes.

Another aspect to which little attention has been paid is the significance of developmental features in determining phylogenetic associations. Larvae of *Nematoscelis* are often difficult to separate as to species. The taxonomy of the larvae is yet to be worked out because the recognized adult characteristics are of no use in the larval identification. Gopalakrishnan (1973) summarized the available information on the sequential morphological development of an individual species. As Gordon (1955) and others have pointed out, larval characteristics may be more useful than those of adults in recognizing phylogenetic interrelationships of species. Adults show a greater degree of differentiation than the larvae, and their characters are more useful in the identification of the species than determining phylogeny. Moreover, part of the morphological variability observed in adults is sometimes ascribed to non-genetic modification that probably has no phylogenetic significance. Usually phylogenetic interrelationships are summarized in a classification. In this connection, larval characters are used

<sup>1</sup>Scripps Institution of Oceanography, La Jolla, CA 92037; present address: Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1346, Kaneohe, HI 96744.

extensively in classifying insect groups, such as Diptera and Hymenoptera. It is the intention of this taxonomic study to provide as much information as possible so that one can examine the systematic value of both larval and adult characters of *Nematoscelis*.

## MATERIAL AND METHODS

The material used in this study consisted of 286 Isaacs-Kidd Mid-water Trawl (10 feet) collections and 1,950 plankton samples, including those collected during the International Indian Ocean Expedition (1960-65). These materials came from different geographical regions of the Atlantic, Indian, and Pacific oceans, mostly between lat. 40°N and 40°S. They are deposited at the Scripps Institution of Oceanography, La Jolla, Calif. All the trawl collections were not quantitative for estimating species abundance. A paper on the distribution and abundance of *Nematoscelis* based on plankton samples was already published (Gopalakrishnan 1974). Measurements were taken on 55 adult morphological characters for examining relative degree of differences. Ten males and ten females of each species were selected for these measurements. Statistical significance was determined on the basis of nonoverlapping confidence levels (95%) of the means. For making drawings, 10-20 individuals of each species were treated in heated 10% aqueous KOH to remove nonchitinous tissues. They were then stained in 1% aqueous Chlorazol Black E. Materials treated in KOH solution could be kept in 60-80% glycerol without shrinkage. Drawings were made with the aid of a camera lucida fitted to monocular and binocular microscopes.

The larval key was prepared on the basis of furcilia characters only. However, a few comments are made on characters of calyptopis and juvenile stages thought to have some diagnostic value. The adult key was prepared based on features of the first thoracic leg (maxilliped), eyes, antenna, and the carapace. Diagnostic features of the petasma are also included in the present key. Many characters are, therefore, used in the present key to facilitate its use on juveniles and adults of both sexes. Most of the commonly used adult characters are illustrated in Figure 1a. The terminology used here is the same that has been followed by most other workers. Larval terminology is defined and described in Gopalakrishnan (1973).

## RESULTS

### Larval Development

Between hatching and sexual maturity all species of *Nematoscelis* pass through four developmental phases: metanauplius, calyptopis, furcilia, and juvenile. A modified version of the nomenclature of larval development of euphausiids is given in Gopalakrishnan (1973). The metanauplius phase consists of one developmental stage, calyptopis of three ( $C_1$ ,  $C_2$ , and  $C_3$ ) and furcilia of three ( $F_1$ ,  $F_2$ , and  $F_3$ ). The strong differentiation of mouth parts and other thoracic legs shows similarities among larvae of all species of this genus. The development of larvae follows either of two pathways: *N. difficilis* and *N. megalops* follow one pathway and the other five species follow the other. During the third furcilia stage the second thoracic leg develops spines on both dactylus and propodus in *N. difficilis* and *N. megalops*, whereas in the rest of the species spines develop only on the dactylus. In all species of *Nematoscelis* this leg becomes the longest of all thoracic appendages.

Other developmental differences between the two species groups are as follows: during the juvenile phase, the maxillules of *N. difficilis* and *N. megalops* develop pseudexopods from the posterior face of the coxa as the four-setose larval exopods disappear; but in the remaining species, at about the same stage, the larval exopod disappears without the development of a pseudexopod. The lacina externa (lobes of basis) of the maxilla is trilobed in larvae of all species, but becomes bilobed in adults of *N. difficilis* and *N. megalops* and single lobed in adults of the remaining species.

The differences in the sequential development of pleopods and telson spines (terminal) are summarized in Figure 2. These features are consistent and appear to be characteristic of each subgroup. The terminal spines of the telson in species of both subgroups show differences not only in their sequential reduction but also in their external morphology (Figure 3A). This structural difference can be seen even during calyptopis stages of all species of this genus. This is a diagnostic feature and may have significance in understanding the evolution of the larvae. The dorsal keel and rostrum of the carapace also appear to be of important diagnostic value for furcilia (Figure 3B)



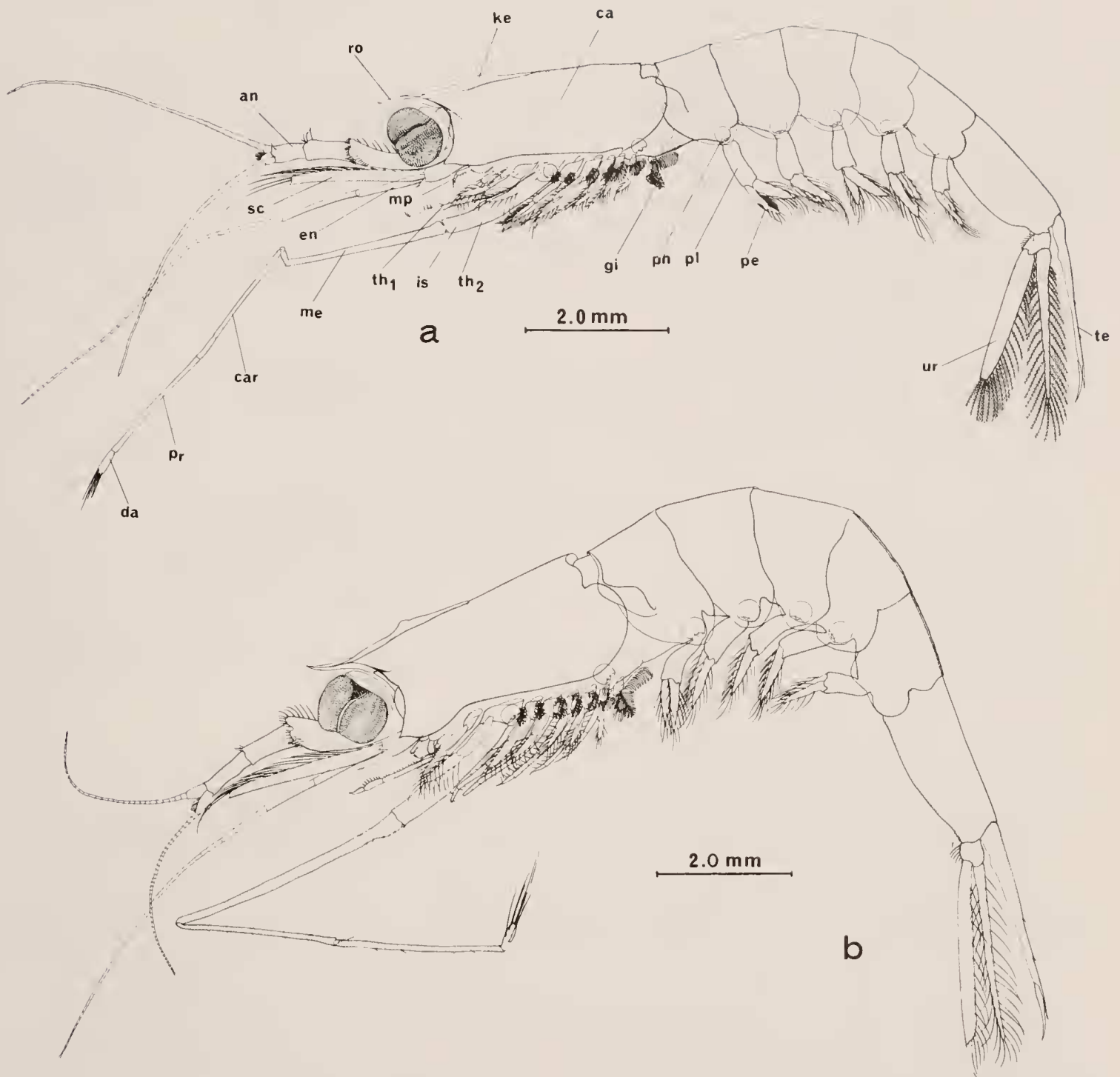


FIGURE 1.—*a. Nematoscelis atlantica*, male (length = 13.2 mm; Indian Ocean, position: lat. 28°08'S, long. 66°09'E); *b. N. microps*, female (length = 16.3 mm; Indian Ocean, position: lat. 10°06'S, long. 41°51'E). *an*, antennule; *ca*, carapace; *car*, carpus of second leg; *da*, dactylus of second leg; *en*, endopod of antenna; *gi*, gill; *is*, ischium of second leg; *me*, merus of second leg; *mp*, mandibular palp; *pe*, petasma; *ph*, photophore; *pl*, pleopod; *pr*, propodus of second leg; *ro*, rostrum; *sc*, scale of antenna; *te*, telson; *th*<sub>1</sub>, first thoracic leg; *th*<sub>2</sub>, second thoracic leg; *ur*, uropod.

The furcilia phase of *Nematoscelis* was defined in Gopalakrishnan (1973) as follows: compound eyes no longer under carapace, but project outside; antenna retains larval natatory function; pleopod becomes functional, each appears first as non-setose rudiment which develops setae at following

moult; furcilia, therefore, with different states of development of pleopods. The following key for identifying furcilia larvae to species is based mostly on diagnostic features of the carapace. There are three developmental stages in the furcilia phase.

GENUS NEMATOSCELIS G.O.SARS

N. LOBATA HANSEN  
 N. GRACILIS HANSEN  
 N. MICROPS G.O.SARS  
 N. ATLANTICA HANSEN  
 N. TENELLA G.O.SARS

N. DIFFICILIS HANSEN  
 N. MEGALOPS G.O.SARS

SEQUENTIAL DIFFERENTIATION OF PLEOPODS

NUMBER OF  
 TELSON SPINES  
 (TERMINAL)

NUMBER OF  
 TELSON SPINES  
 (TERMINAL)

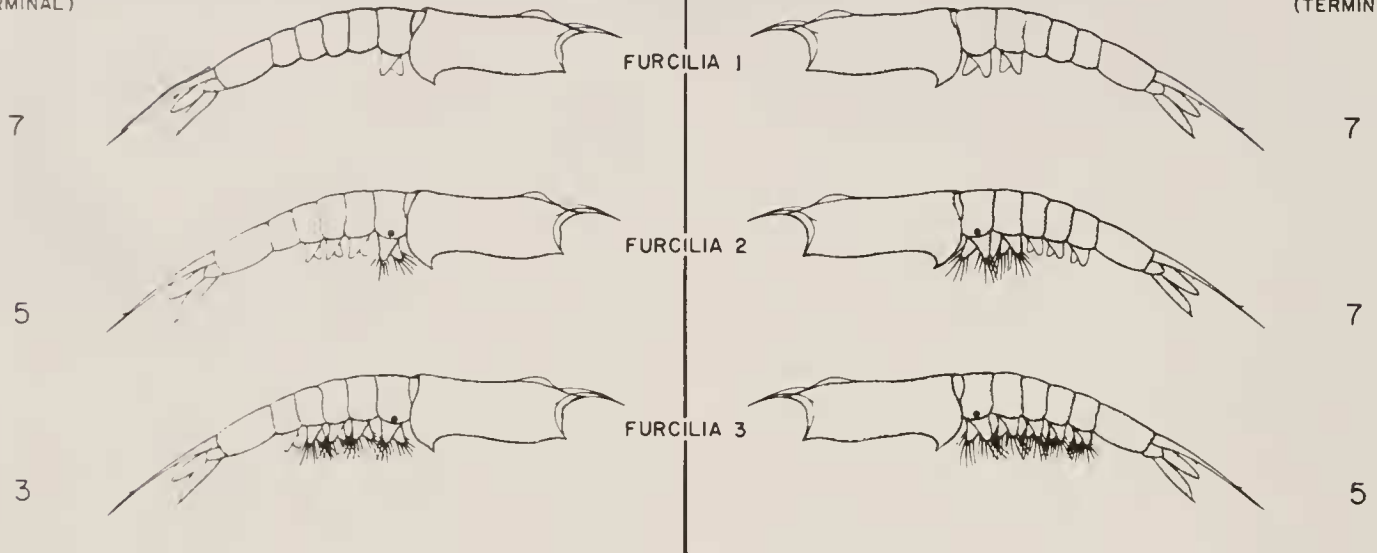


FIGURE 2.—Developmental sequence of differentiation of pleopods and terminal spines of the telson in species of *Nematoscelis* (adapted from Gopalakrishnan 1973).

Key for Identifying Furcilia Larvae of *Nematoscelis*

- 1a. Each terminal spine of telson with a pair of conspicuous lateral subspines (Figure 3A,a); setules present only above these subspines. F<sub>1</sub> stage with seven terminal spines and one pair of non-setose pleopods; F<sub>2</sub> with five terminal spines, one pair of setose pleopods and three pairs of non-setose pleopods; F<sub>3</sub> with three terminal spines, four pairs of setose pleopods and one pair of non-setose pleopods (Figure 2) ..... 2
- 1b. Each terminal spine of telson without subspines, but with lateral setules along three-fourths of its length (Figure 3A,b). F<sub>1</sub> stage with seven terminal spines and two pairs of non-setose pleopods; F<sub>2</sub> stage also with seven terminal spines but two pairs of setose pleopods and three pairs of non-setose pleopods; F<sub>3</sub> stage with five terminal spines and five pairs of setose pleopods (Figure 2) ..... 5
- 2a. Rostrum rectangular with truncated anterior end (Figure 3B,b,c) ..... 3
- 2b. Rostrum triangular with pointed anterior end (Figure 3B,a,d) ..... 4
- 3a. Carapace keel very large and hump shaped; rostrum usually curved downwards (Figure 3B,b); length of sixth abdominal segment relatively short and its ventral margin largely convex ..... *N. tenella*
- 3b. Carapace keel small, usually triangular shaped (Figure 3B,c); ventral margin of sixth abdominal segment not convex ..... *N. gracilis*
- 4a. Rostrum broad and stough, keel large and platelike; carapace compressed anteroposteriorly (Figure 3B,a) ..... *N. microps*
- 4b. Rostrum elongate and slender; keel less conspicuous (Figure 3B,d) ..... *N. atlantica*
- 5a. Rostrum broad, thick and triangular (Figure 3B,e) ..... *N. megalops*
- 5b. Rostrum slender and narrow (Figure 3B,f) ..... *N. difficilis*

Furcilia larvae of *N. atlantica* and *N. lobata* are difficult to separate. More samples are necessary to

complete the larval description of *N. lobata*. This species is known to occur only in the semi-isolated

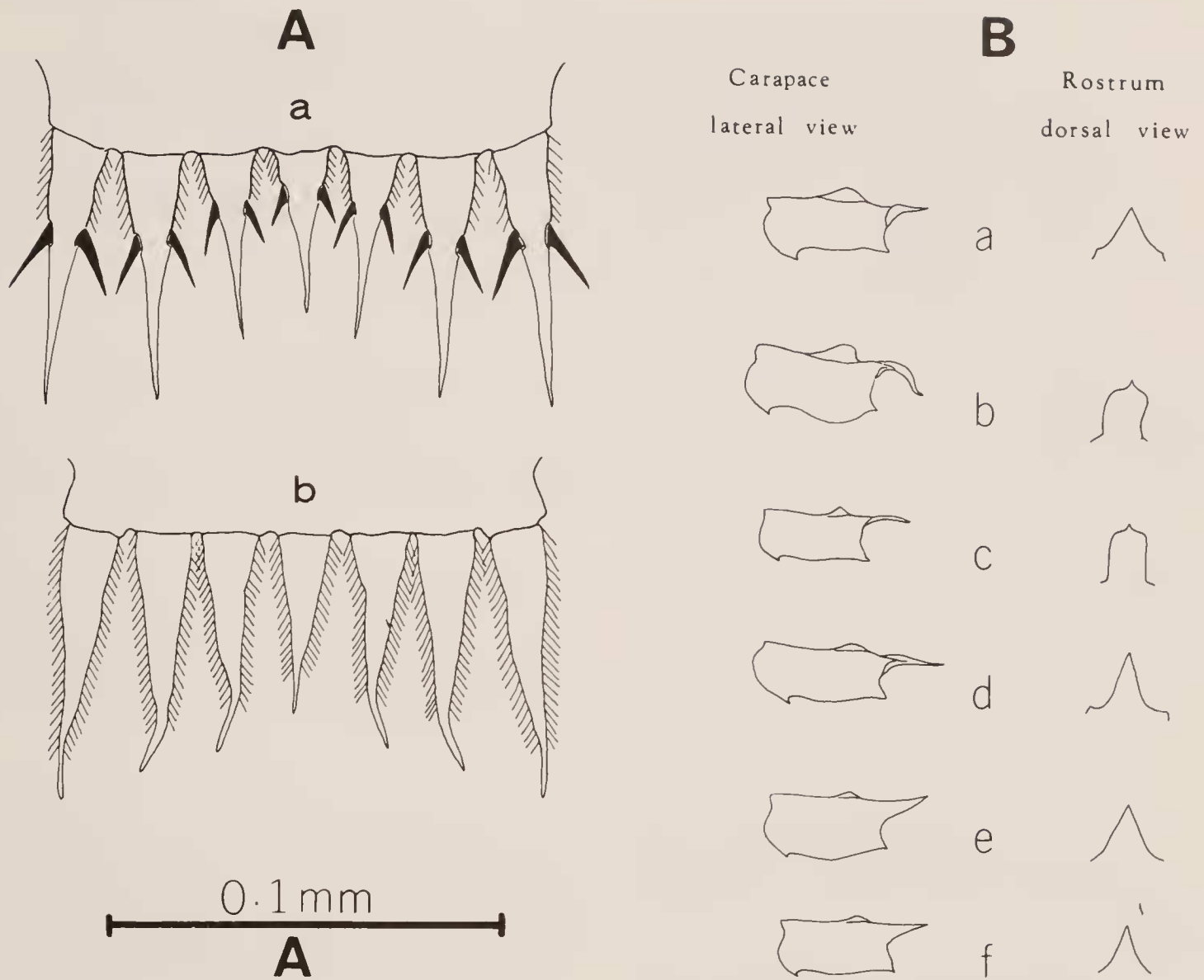


FIGURE 3.—A, terminal spines on larval telson: a, *Nematoscelis gracilis*, *N. microps*, *N. tenella*, *N. atlantica*, and *N. lobata*; b, *N. difficilis* and *N. megalops*. B, carapace and rostrum of furcilia larvae of *Nematoscelis*: a, *N. microps*; b, *N. tenella*; c, *N. gracilis*; d, *N. atlantica*; e, *N. megalops*; f, *N. difficilis*.

Sulu and Celebes seas in the region of the Indo-Australian Archipelago (Gopalakrishnan 1974). The distribution of *N. atlantica* appears not to extend into this area. Within each species, the body sizes of metanauplii ranged from 0.8 to 1.0 mm. However, body size differences among all

species became apparent from the first calyptopis stage onwards (Table 1). It is at this stage that the larvae start feeding (Gopalakrishnan 1973). Evidently *N. tenella* larvae are the smallest, and *N. megalops* the largest. Length measurements of furcilia larvae also show size differences among

TABLE 1.—Body lengths (mm) of calyptopis stages of *Nematoscelis*. (Medians were based on 10 to 36 individuals of each species for each stage.)

Species	Stage 1		Stage 2		Stage 3	
	Median	Range	Median	Range	Median	Range
<i>N. gracilis</i>	1.4	1.3-1.4	2.1	2.0-2.2	2.6	2.5-2.7
<i>N. microps</i>	1.4	1.3-1.4	2.0	2.0-2.1	2.7	2.6-2.8
<i>N. atlantica</i>	1.5	1.4-1.5	2.2	2.1-2.3	2.8	2.6-2.9
<i>N. tenella</i>	1.2	1.2-1.3	1.8	1.7-1.9	2.5	2.4-2.7
<i>N. megalops</i>	1.6	1.5-1.7	2.4	2.1-2.5	3.2	2.9-3.3
<i>N. difficilis</i> <sup>1</sup>	1.4	1.3-1.5	2.0	1.9-2.1	2.8	2.2-2.8

<sup>1</sup>Data taken from Gopalakrishnan (1973).



TABLE 2.—Body lengths (mm) of furcilia stages of six species of *Nematoscelis*.  
(Medians were based on 6 to 20 individuals of each species for each stage.)

Species	Stage 1		Stage 2		Stage 3	
	Median	Range	Median	Range	Median	Range
<i>N. gracilis</i>	2.8	2.6-3.0	3.0	2.9-3.4	3.3	3.2-3.5
<i>N. microps</i>	2.9	2.6-3.1	3.2	3.0-3.3	3.5	3.3-3.5
<i>N. atlantica</i>	3.4	3.2-3.5	3.9	3.9-4.1	4.3	4.2-4.5
<i>N. tenella</i>	2.7	2.6-2.9	3.2	3.1-3.3	3.5	3.5-3.6
<i>N. megalops</i>	3.7	3.6-4.0	4.3	4.2-4.3	4.8	4.7-5.0
<i>N. difficilis</i> <sup>1</sup>	3.1	2.7-3.2	3.5	3.4-3.7	3.9	3.6-4.2

<sup>1</sup>Data taken from Gopalakrishnan (1973).

species (Table 2). Between the species pair *N. megalops* and *N. difficilis*, there is a significant size difference during both the calyptopis and furcilia stages.

Juveniles of all species of *Nematoscelis* are identified on the basis of their morphological similarities to adults, especially in such characters as the carapace, the rostrum, and the eye. During the juvenile stages of *N. tenella*, the carapace becomes elongate and narrow as in adults; the dorsal keel on the carapace elongates anteriorly and posteriorly; the broad and curved larval rostrum becomes short and pointed; and the larval eye develops narrow upper and lower lobes (in the adult eye only the lower lobe remains narrow). These diagnostic features help to distinguish juveniles of *N. tenella* from similar stages of other species.

The propodus of the first thoracic leg (maxilliped) is a useful character to identify juveniles, as it is in adults. Although the number of setae on the propodus of this leg is fewer in juveniles than in adults, it is possible to examine the differences in the "style" of setation among juveniles of *Nematoscelis*. For example, in adults of *N. gracilis* there are two rows of setae on the propodus of the maxilliped (Figure 6c); in the juvenile stage this segment develops at least one seta from each position of these two rows. In *N. atlantica* the

same segment has only one row (marginal) of setae in adults, and in juveniles at least one seta is present at the position of this marginal row. This difference in the style of setation can be used to distinguish *N. gracilis* and *N. atlantica* juveniles. The propodus of the maxilliped of *N. microps* also has one row of marginal setae, but its inner margin is convex; the carpus of this appendage is shorter than its propodus. The prominent dorsal keel on the carapace is a good diagnostic feature of *N. microps* juveniles.

#### *Nematoscelis* G. O. Sars—Generic Characters

The shape of the rostrum variable in males and females; eyes large and bilobed; the peduncle of the first antenna slender in females and thicker in males. Dactylus of the first thoracic leg (maxilliped) triangular, flattened and furnished with comblike setae on its inner lateral margin. The second pair of legs greatly produced and with spines on the distal segment or on both the penultimate and the distal segments. The endopod of the seventh leg biarticulate in the female, lacking in the male. Eighth leg a simple setose plate. All the four processes—proximal, terminal, lateral, and spine-shaped process—present in the petasma; the spine-shaped process always straight and the lateral without any hooks.

#### Key for Identifying Adult Species of *Nematoscelis*

The following key is adopted from Hansen (1910, 1912), Boden (1954), Boden et al. (1955), and Mauchline and Fisher (1969). It is modified to include additional information:

- 1a. Second pair of thoracic legs with long spines from both terminal segment (dactylus) and distal end of propodus. Third to sixth thoracic legs with three segments beyond knee. Maxillule with well-developed pseudexopod. Basis of maxilla bilobed. Ventrolateral spine on coxa of antenna greatly produced (Figure 4A,e,f). Carapace with conspicuous cephalic ridge (Figure 5f,g). Eyes large (Figure 4B,e,f). Propodus of first thoracic leg with setae

- arranged in three rows (Figure 6e,f). Proximal process of petasma with serrations in two rows (Figure 7a,b) ..... 2
- 1b. Second pair of thoracic legs with long spines from terminal segment (dactylus) only. Third to fourth thoracic legs with only two segments beyond knee, and fifth and sixth with only one. Maxillule without a pseudexopod. Basis of maxilla with one lobe only. Ventrolateral spine on coxa of antenna small or greatly reduced (Figure 4A,a-d). Cephalic ridge on carapace absent or inconspicuous (Figure 5a-e). Eyes relatively small (Figure 4B,a-d). Propodus of first leg with setae arranged in one or two rows (Figure 6a-d). Proximal process of petasma without serrations, or when present in one row only (Figures 7c and 8) ..... 3
- 2a. Proximal process of petasma reaching almost middle of serrated margin of terminal process (Figure 7a). Serrated part of terminal process slightly curved towards median lobe. Propodus of first leg usually with six setae in outer (dorsal) row and five in middle row ..... *N. megalops*
- 2b. Proximal process reaching much beyond middle of distal part of terminal process (Figure 7b). Distal end of terminal process greatly curved towards median lobe, reaching slightly over distal end of proximal process. Propodus of first leg usually with five setae in dorsal row and four in middle row ..... *N. difficilis*
- 3a. Propodus of first thoracic leg with setae arranged in two separate rows (Figure 6c,d). Lateral process of petasma much longer than both terminal and spine-shaped processes (Figures 7c and 8a). Distal end of lateral process serrated. .... 4
- 3b. Propodus of first thoracic leg dorsoventrally flattened and furnished with setae in one row only (Figure 6a,b). Lateral process of petasma much smaller than both terminal and spine-shaped processes (Figure 8b-d). No serrations on lateral process or any other processes of petasma ..... 5
- 4a. Ventrolateral spine on coxa of antenna highly reduced to a hump (Figure 4A,d). Lower part of eye much smaller than upper part (Figure 4B,d). A long seta projecting from dorsal surface of dactylus of first thoracic leg (Figure 6d). Distal end of lateral process always reaching beyond distal end of proximal process (Figure 8a)..... *N. tenella*
- 4b. Ventrolateral spine on coxa of antenna not reduced to a hump (Figure 4A,a). Lower part of eye larger than or nearly equal to upper part (Figure 4B,a). No seta on dorsal surface of dactylus of first thoracic leg (Figure 6c). Distal end of lateral process not reaching beyond distal end of proximal process (exception: "old forms" from the Pacific Ocean to be discussed in a later section) (Figure 7c)..... *N. gracilis*
- 5a. Upper part of eye slightly narrower than lower part (Figures 4B,b and 9c). Propodus of first thoracic leg with less convex inner margin (Figure 6b and 9d). Keel on carapace less prominent and without conspicuous hump. Abdominal segments without any elevated dorsal keels. Shapes and relative lengths of processes of petasma as shown in Figure 8c,d. Lengths of propodus and carpus of first leg nearly equal ..... 6
- 5b. Upper lobe of eye slightly wider than lower lobe; lateral evagination much deeper in upper than in lower lobe (Figure 4B,c). Propodus of first thoracic leg with highly convex inner margin (Figure 6a). Keel on carapace quite prominent and with conspicuous hump (Figures 5c and 1b). Fourth and fifth abdominal segment characterized by less elevated dorsal keels. Carpus of first leg shorter than propodus. Shapes and relative lengths of processes of petasma as shown in Figure 8b..... *N. microps*
- 6a. Proximal process thick; terminal process much shorter than both proximal and spine-shaped processes. Lateral process small. Median lobe greatly flattened and broad; its outer and inner margins broadly convex, inner margin forming an acute distal angle with outer margin (Figure 8c). Adult female without lateral denticle on carapace..... *N. lobata*
- 6b. Proximal process thin, a little shorter than terminal process; lateral process slightly curved toward median lobe, its distal end reaching to or almost to distal end of proximal process (Figure 8d). Adult female with lateral denticle on carapace..... *N. atlantica*

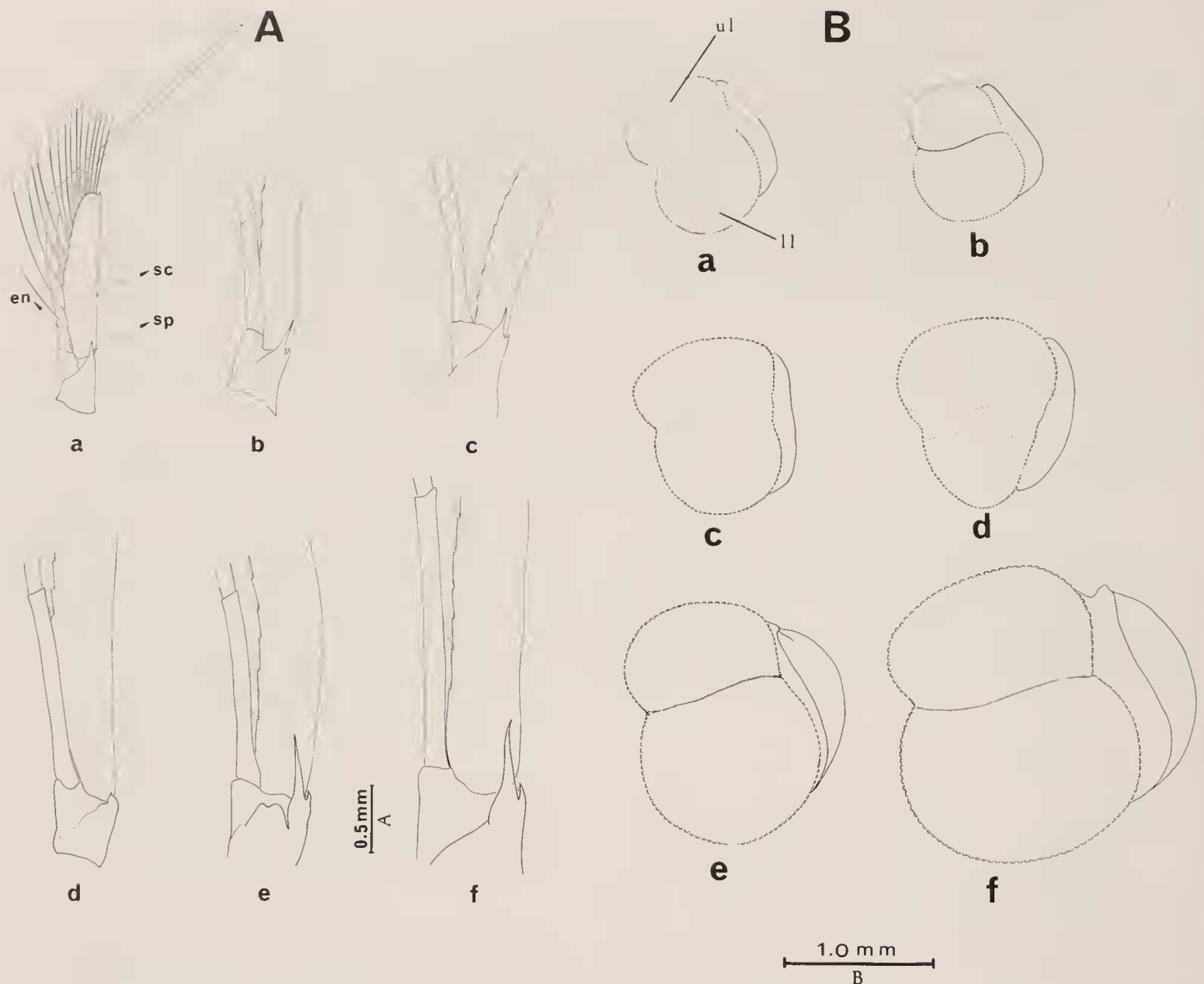


FIGURE 4.—A, antenna (ventral view) and B, eye (lateral view) of *Nematoscelis*: a, *N. gracilis*; b, *N. atlantica*; c, *N. microps*; d, *N. tenella*; e, *N. difficilis*; f, *N. megalops*. en, endopod; sc, scale; sp, spine on proximal segment of protopod; ul, upper lobe; ll, lower lobe.

The present study shows that there are two distinct forms in *Nematoscelis gracilis*. They are distinguished as ecophenotypes and are referred to here as the "old form" and the "new form." The old form is identical in morphological characters with the typical form described by Hansen (1910) from the waters of the Indo-Australian Archipelago, and the new form is distinguished from the typical form on the basis of morphological differences on the proximal process of the petasma. There is also an apparent size difference between the two forms: Body length of the old form is significantly larger than that of the new form (cf. Figure 5a,b). The upper lobe of eye in the new form is slightly narrower than that in the old form. Both forms are distinguishable only

as adults. The old form occurs mostly in the northern section of the tropical Indo-Pacific subregion and has maximum abundance in the oxygen-poor waters of the Arabian Sea, Bay of Bengal, and eastern tropical Pacific Ocean. The new form occurs in the region of the South Equatorial Current. Along the equatorial zone, where the two forms overlap, an "intermediate" of the two forms, with regard to the length of the proximal process of petasma, is also encountered. Geographical distributions of these forms are described in Gopalakrishnan (1974). There are apparent morphological differences between the old forms of the Indian and Pacific oceans. The following key is prepared for identifying the forms of *N. gracilis*:



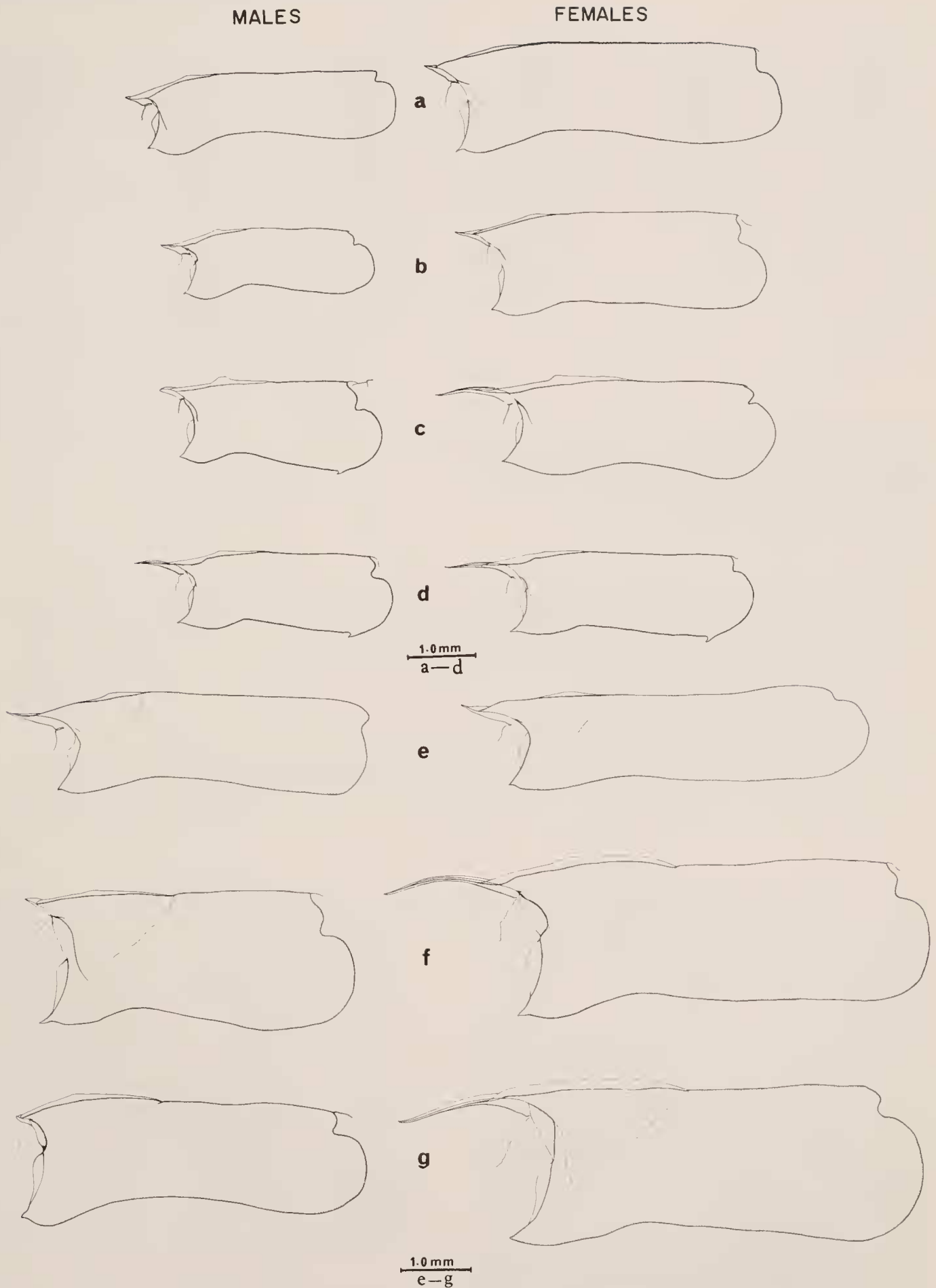


FIGURE 5.—Carapace of *Nematoscelis*: a, *N. gracilis* "old form" (length: male = 15.1 mm, female = 16.9 mm); b, *N. gracilis* "new form" (length: male = 11.7 mm, female = 15.0 mm); c, *N. microps* (length: male = 15.3 mm, female = 17.0 mm); d, *N. atlantica* (length: male = 12.9 mm, female = 13.7 mm); e, *N. tenella* (length: male = 18.0 mm, female = 19.1 mm); f, *N. difficilis* (length: male = 19.0 mm, female = 23.4 mm); g, *N. megalops* (length: male = 21.7 mm, female = 25.2 mm).

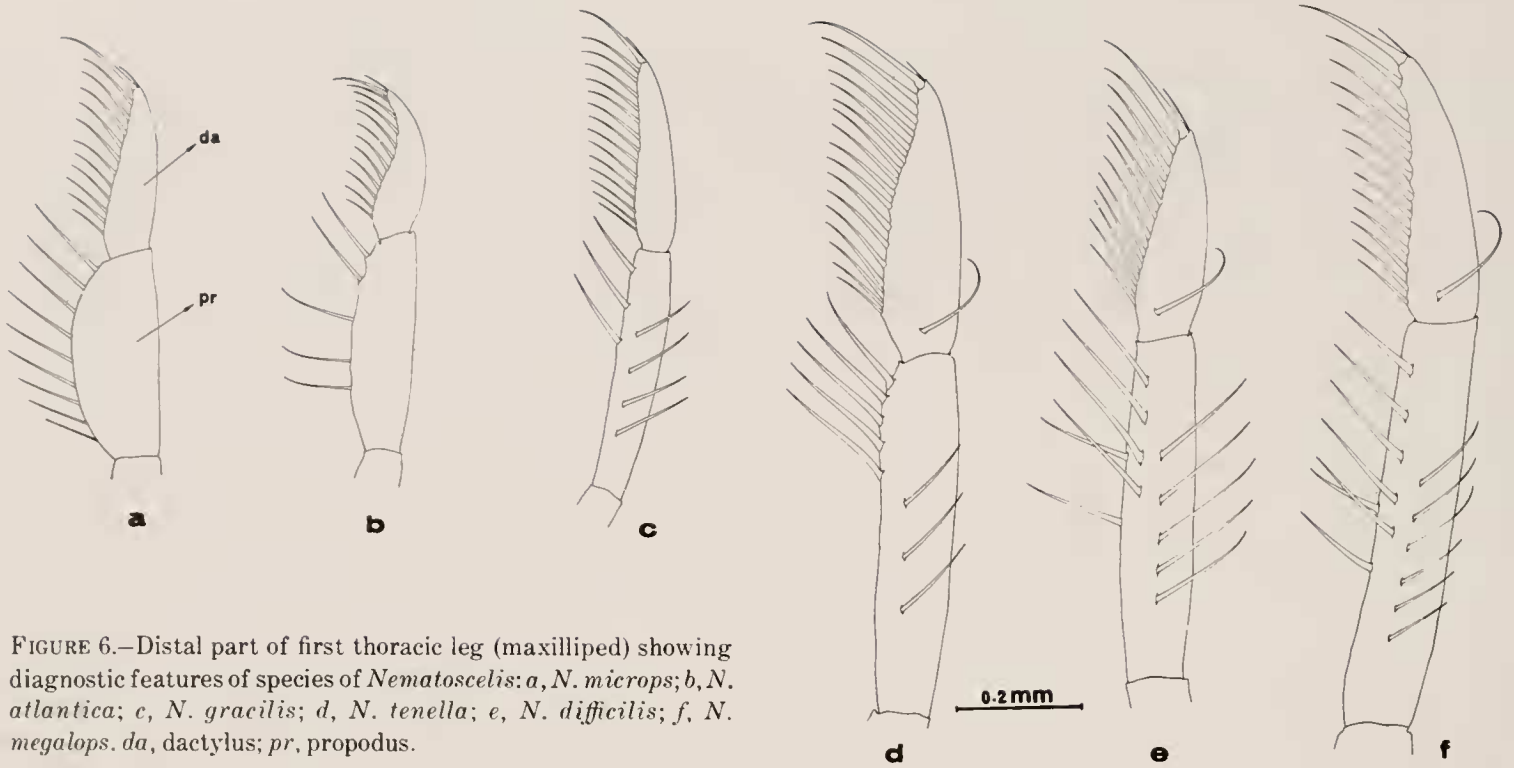


FIGURE 6.—Distal part of first thoracic leg (maxilliped) showing diagnostic features of species of *Nematoscelis*: a, *N. microps*; b, *N. atlantica*; c, *N. gracilis*; d, *N. tenella*; e, *N. difficilis*; f, *N. megalops*. da, dactylus; pr, propodus.

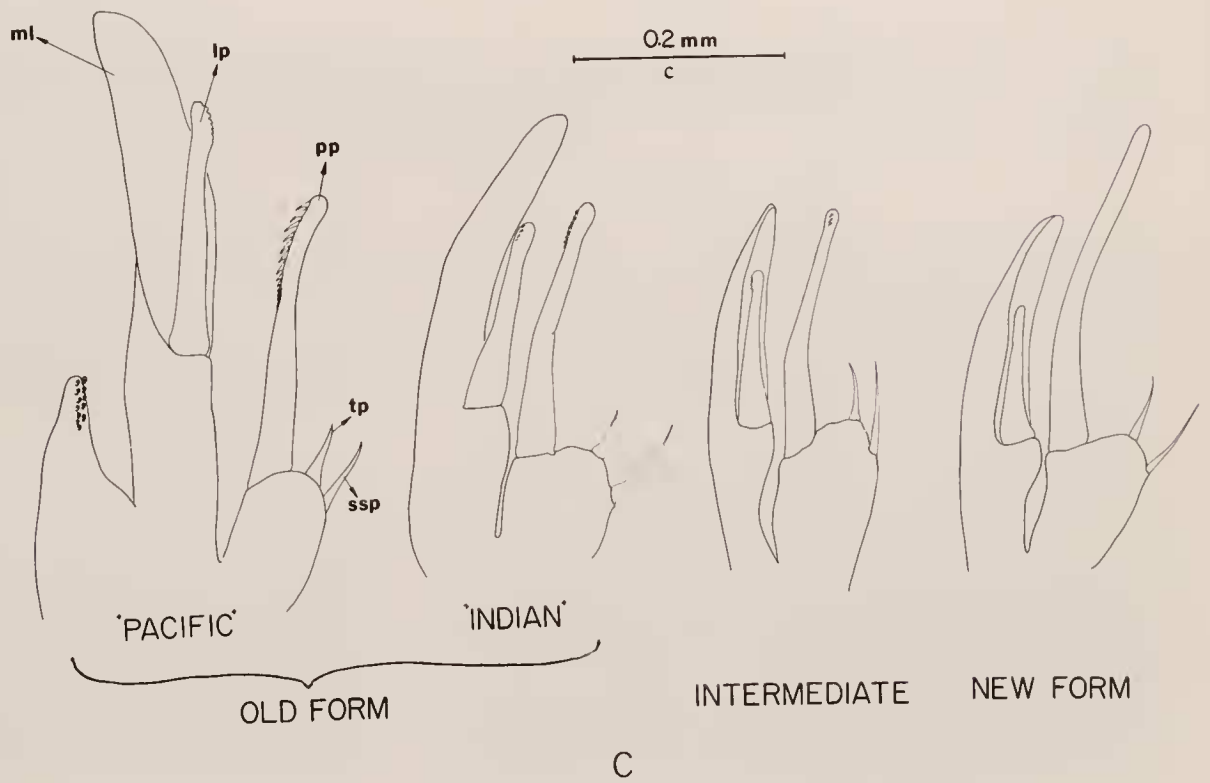
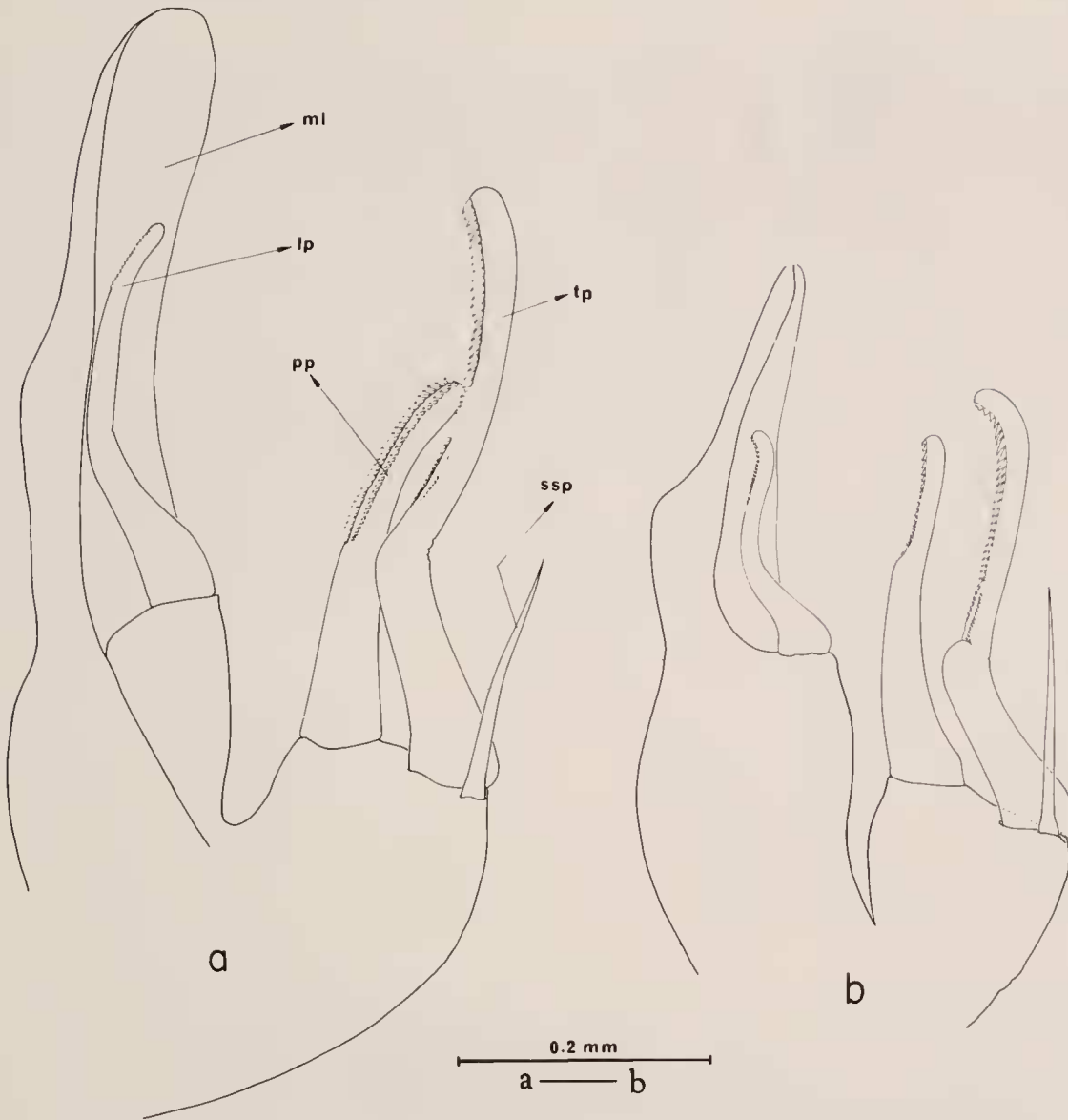
- i. Distal end of lateral process always reaching far beyond distal end of proximal process; proximal process strongly serrated (average number of teeth 10) (Figure 7c) . . . . Pacific old form
- ii. Distal end of proximal process always reaching beyond distal end of lateral process, but not reaching distal end of median lobe; proximal process moderately serrated (average number of teeth 6) (Figure 7c) . . . . . Indian old form
- iii. Proximal process extremely long, reaching far beyond distal end of median lobe. Proximal process without any serrations (Figure 7c) . . . . . new form
- iv. Proximal process much longer than lateral process, its distal end reaching as far as distal end of median lobe. Proximal process slightly serrated (average number of teeth 3) (Figure 7c) . . . . . intermediate of old and new forms

The two forms of *N. gracilis* can also be separated with certainty by plotting the ratio of the proximal process to the median lobe of petasma against carapace length (Figure 10). The intermediate forms represent the presumed intergradation of new and old forms, although they appear to be much closer to the old form than to the new form with respect to this character. The difference in body lengths between old forms of the Indian and Pacific oceans is also apparent from this figure. Table 3 shows results of an analysis of covariance on proximal process of the petasma and carapace length of *N. gracilis* old and new forms. Length of the proximal process of petasma of the old form is significantly different statistically from that of the new form. Body lengths of the old forms in the Pacific and Indian oceans are significantly different statistically. Both intermediate and new forms are smaller than the old

forms. Lengths of both the median lobe and lateral process are also different in these forms.

Of the 55 morphological characters measured, many showed statistically significant differences between species pairs. For example, the following characters of *N. gracilis* were different from those of *N. microps*: basal length of keel; length of carpus of first thoracic leg; lateral length of carapace; length of carapace between apex of keel and its posterolateral margin; length of carapace between apex of keel and point above photophore on seventh thoracic segment; distance between photophore on coxa of second thoracic leg and photophore on coxa of seventh thoracic leg; lengths of

FIGURE 7.—Petasmae of *Nematoscelis*: a, *N. megalops*; b, *N. difficilis*; c, *N. gracilis* forms. lp, lateral process; ml, median lobe; pp, proximal process; ssp, spine-shaped process; tp, terminal process.





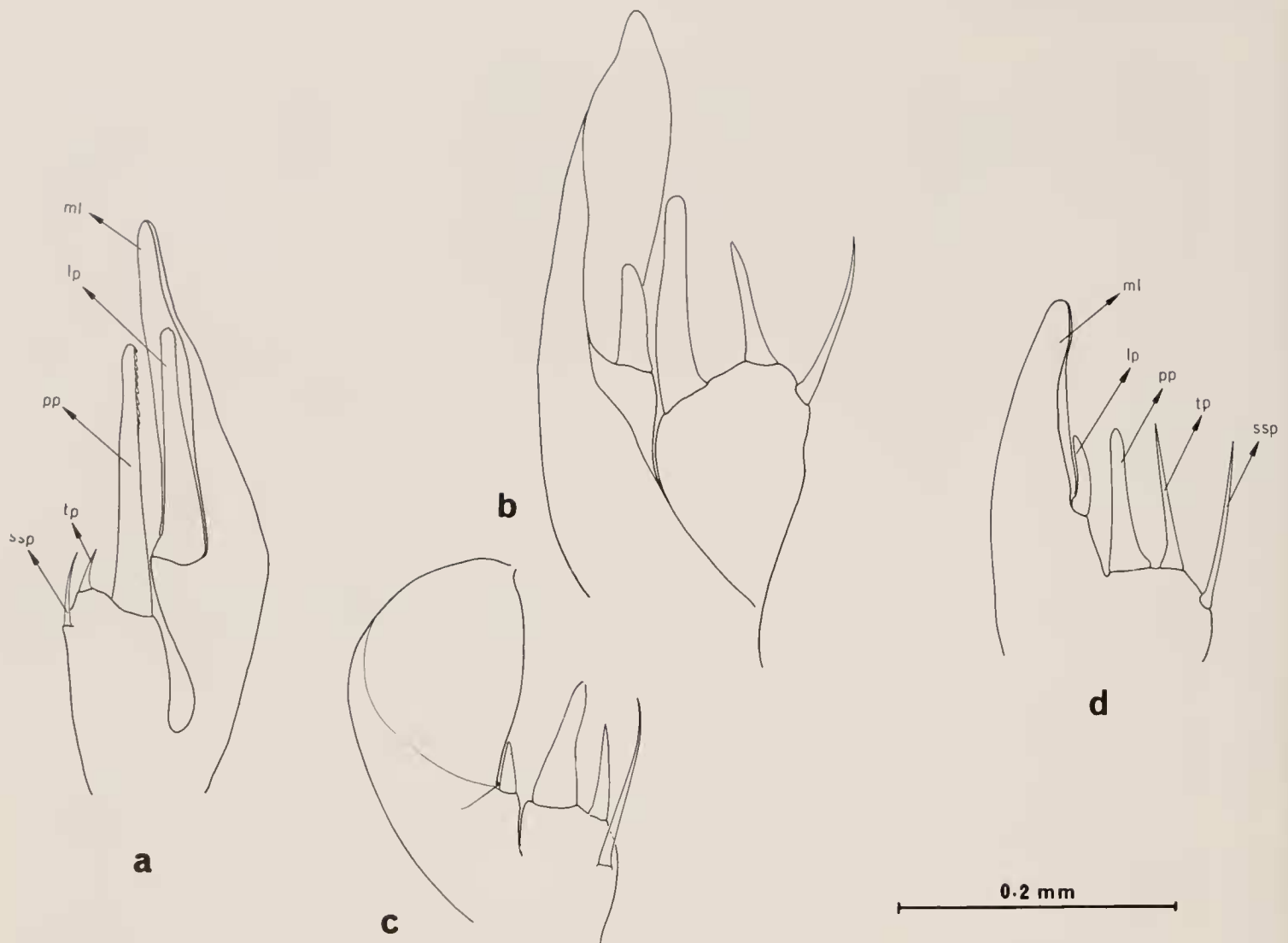


FIGURE 8.—Petasmae of *Nematoscelis*: a, *N. tenella*; b, *N. microps*; c, *N. lobata*; d, *N. atlantica*. lp, lateral process; ml, median lobe; pp, proximal process; ssp, spine-shaped process; tp, terminal process.

TABLE 3.—Analysis of covariance on proximal process of the petasma and carapace length of *Nematoscelis gracilis* "old form" (Indian Ocean) and the "new form."

Source	Sum of squares	Degrees of freedom	Mean square	F ratio	Probability
Proximal process alone:					
Between means	26.934	1	26.934	$F_{1,58} = 328.463$	<0.0001
Within groups	4.786	58	0.082		
Total	31.720	59			
After accounted for differences in carapace lengths:					
Between means	21.136	1	21.136	$F_{1,57} = 289.534$	<0.0001
Within groups <sup>1</sup>	4.186	57	0.073		
Regression (overall)	6.398	1			
Total	31.720	59			

<sup>1</sup>0.600 is within SS (regression) removed.

spine-shaped process, terminal process, proximal process, and lateral process of petasma; basal width of lateral process of petasma; number of marginal setae on exopod of maxilla; number of setae on second segment of mandibular palp. Similarly, *N. atlantica* and *N. microps* differ as

follows: in dorsal length of first abdominal segment; length of keel on carapace; lateral length of sixth abdominal segment; length of carpus of first thoracic leg; width of upper lobe of eye; lateral length of carapace; length of carapace between apex of keel and its posterolateral margin; length

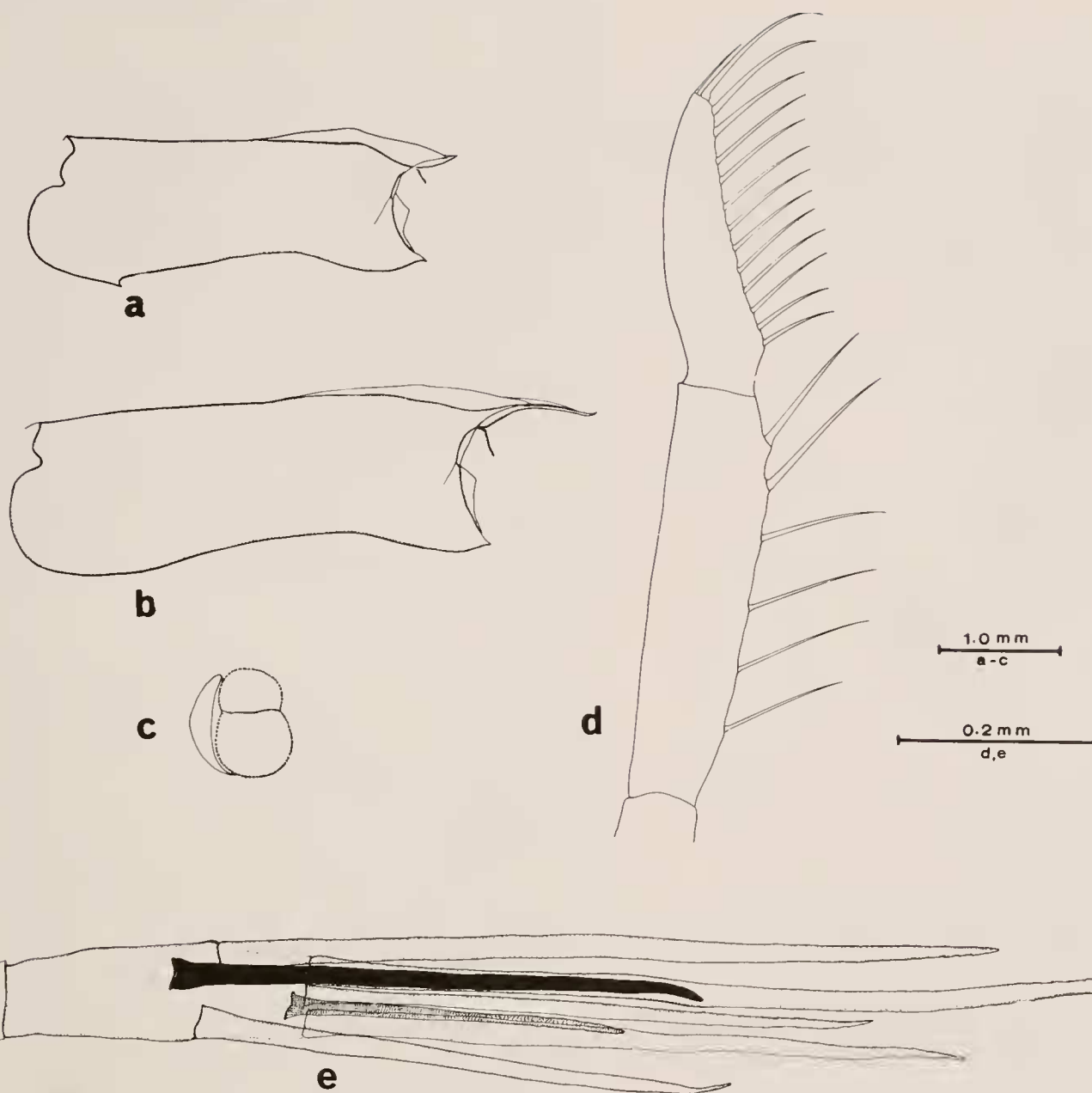


FIGURE 9.—*Nematoscelis lobata*: a, male carapace (body length = 12.1 mm); b, female carapace (body length = 13.5 mm); c, eye; d, distal part (propodus and dactylus) of first thoracic leg (maxilliped); e, dactylus of second thoracic leg showing arrangement of apical spines.

of carapace between apex of keel and the point above photophore on seventh thoracic segment; distance between photophore on coxa of second thoracic leg and photophore on coxa of seventh thoracic leg; length of proximal process of petasma; basal widths of lateral and proximal processes of petasma.

*Nematoscelis tenella* differs from other species in length of carpus of second thoracic leg, width of lower lobe of eye, lengths of merus and propodus of second thoracic leg, length of lateral spine of protopod of antenna, lengths of spine-shaped process and terminal process of petasma and basal widths of spine-shaped process and terminal process of petasma.

The lengths of the spine-shaped process and proximal process of the petasma and number of marginal setae on the pseudexopod of the maxillule of *N. difficilis* are different from *N. megalops*. The species pair *N. difficilis*-*N. megalops* differs from other species in the following characters: basal length of keel; length of scale of antenna; lengths of carpus, dactylus, and longest spine on distal end of second leg; lengths of ischium and merus of first thoracic leg; vertical length and width of lower lobe of eye; dorsal length of first abdominal segment; length and basal width of terminal process of petasma; number of marginal setae on exopod of maxilla, endopod and pseudexopod of maxillule, and on

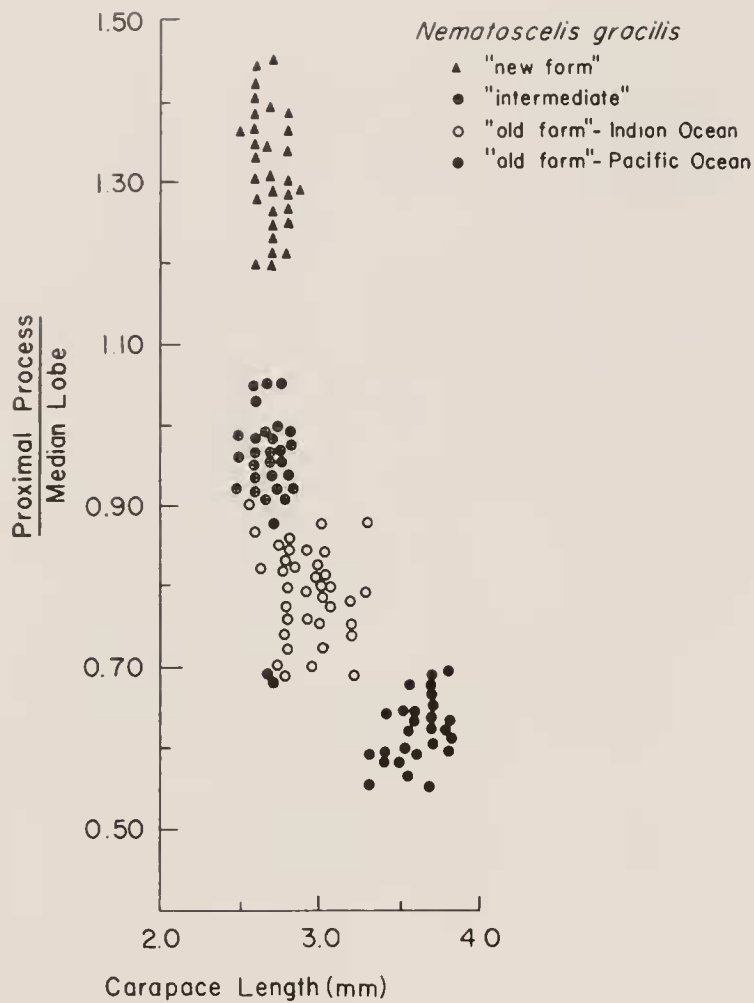


FIGURE 10.—*Nematoscelis gracilis* forms: ratio of proximal process to median lobe of petasma plotted against carapace.

propodus of first thoracic leg; number of marginal spine on lacina externa of maxillule; number of setae on second segment of mandibular palp.

### Sexual Dimorphism in *Nematoscelis*

Sexual dimorphism in euphausiids was best documented by Hansen (1910, 1912). Einarsson (1942) and Nemoto (1966) provided further details. The most sexually dimorphic characters are: the lateral denticle, keel, and rostrum of carapace; antennule; eyes; sixth and seventh thoracic legs; first and second abdominal pleopods; preanal spine.

The states of the lateral denticle, keel, and rostrum in both sexes of *Nematoscelis* are illustrated in Figure 5. The carapace and rostrum are shorter in males than in females. The rostrum in the male is rarely variable; in the female it is always long and slender, except in *N. gracilis* and *N. tenella*. The lateral denticle is absent in all species except in males of *N. microps* and both sexes of *N. atlantica*. McLaughlin (1965) reported the oc-

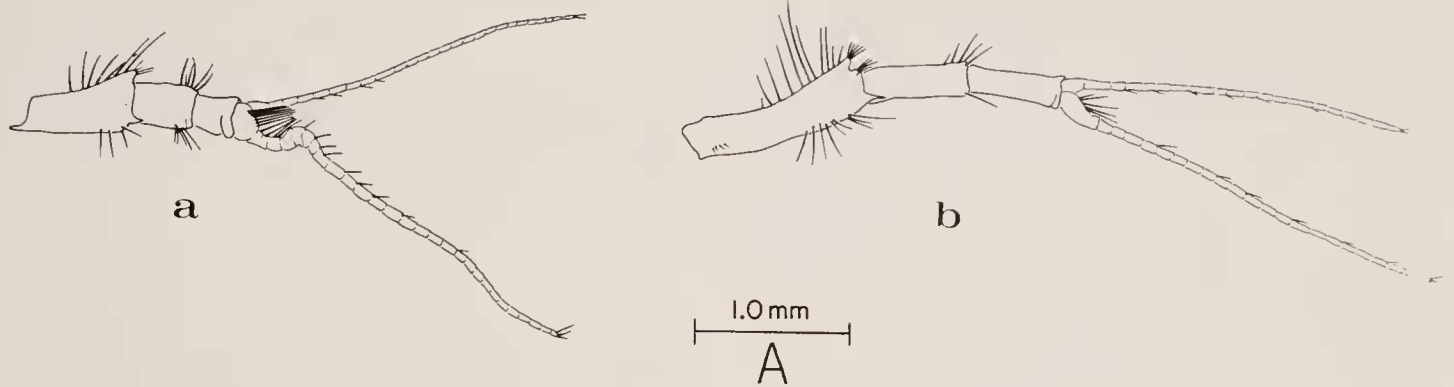
currence of this denticle in both subadult and adult stages of *N. difficilis* caught from the northeastern Pacific Ocean. In the present study, the lateral denticle on the carapace was found only in immature specimens of this species, but not in adults. These individuals were collected from the North Pacific Drift and California Current areas. No sexual dimorphism was observed in the shape of eyes in *Nematoscelis*. The antennular peduncle in males has the two distal segments much thicker than in females; the second segment somewhat shorter and the third segment much shorter than in females (Figure 11A,a,b). The lower flagellum of the antennule has the basal segment much thickened in males and furnished with tufts of sensory setae. In *N. gracilis* males, the proximal part of this flagellum bends downward so as to accommodate the enlarged basal segment (Figure 11A,a).

Sexual dimorphism in abdominal photophores is characteristic of *Nematoscelis*. Einarsson (1942) pointed out a few examples of enlargements of abdominal photophores in this genus. James (1973) reported the existence of this feature in the North Atlantic species of *N. tenella*, *N. atlantica*, and *N. microps*. In the course of examining the material from all oceans, certain interspecific differences of photophore enlargement have become evident. In females of all species of *Nematoscelis*, the photophores on each of the first four abdominal segments are more or less alike in size and shape (Figure 1b). However, in males, one or more of these photophores often show considerable enlargement. The patterns of this enlargement appear to be consistent, species specific, and therefore of diagnostic value.

Associated with photophore enlargement is the occurrence of paired chitinous saddle-shaped plates on the dorsal side of the abdominal segment anterior to that in which the photophore is enlarged (Figure 11B). Types of photophore enlargement in species of *Nematoscelis* are shown in this figure. In the Indian Ocean, *N. gracilis* males have the first abdominal photophore enlarged and lack chitinous plates on the dorsal side of the abdomen. *Nematoscelis microps* males have the second photophore enlarged and either with a dorsal hump (Figure 11B,b) or paired chitinous plates on the dorsal side of the first abdominal segment. Taniguchi (1966) reported occurrence of this hump on *N. microps* collected from the northeastern Indian Ocean. Humped males of this species are frequently found in the tropical



**A**



**B**

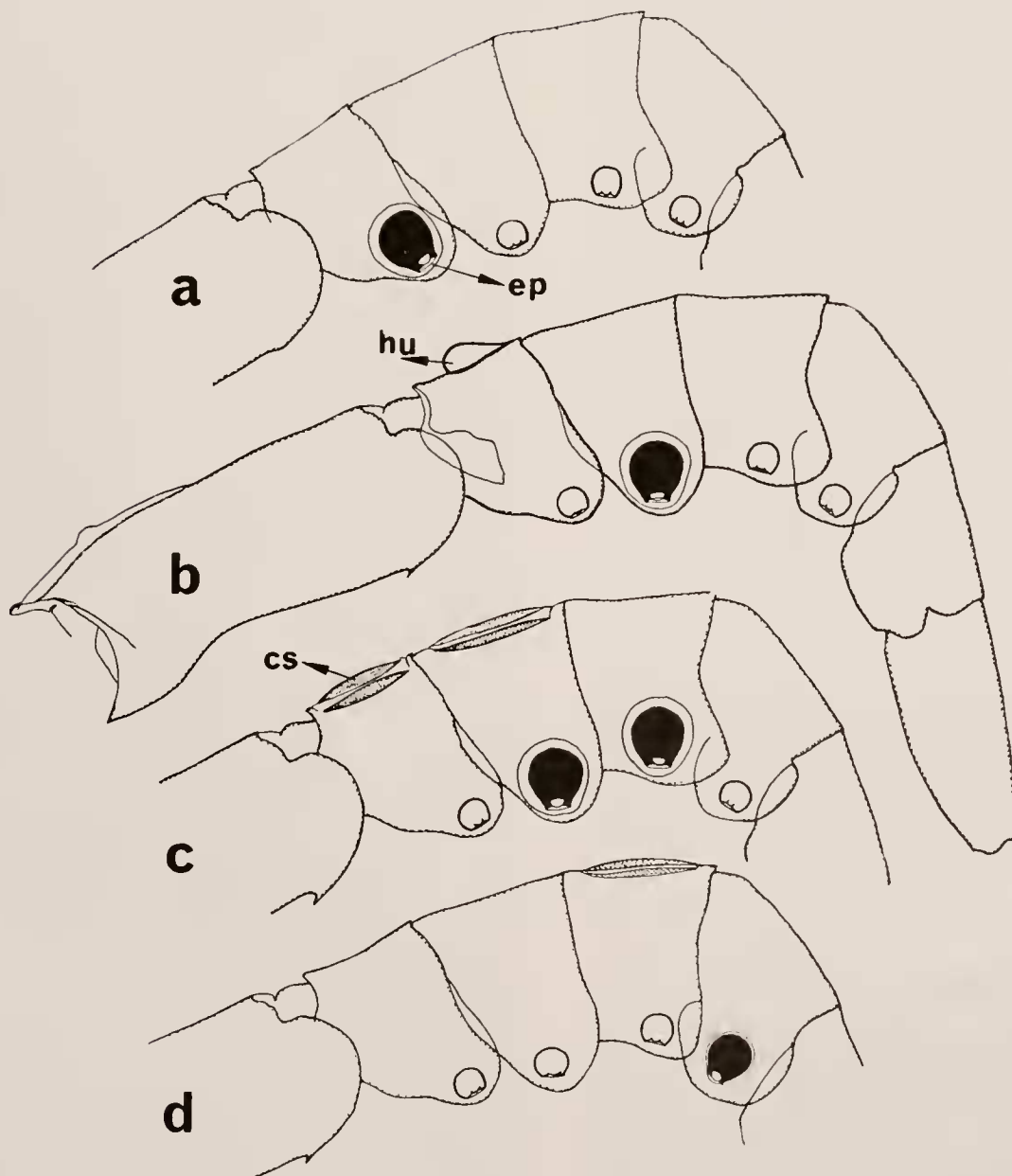


FIGURE 11.—A, dimorphic antennule of *Nematoscelis gracilis*: a, male; b, female. B, enlarged photophores of *Nematoscelis* males: a, *N. gracilis* forms; b, *N. microps*; c, first form of *N. tenella* and *N. atlantica*; d, second form of *N. tenella* and *N. atlantica*. ep, enlarged photophore; hu, dorsal hump; cs, chitinous "saddle."

Indo-West Pacific subregion. *Nematoscelis microps* males with paired chitinous plates on the first abdominal segment occur mostly in the tropical regions of the Pacific, Atlantic, and Indian oceans. James (1973) found this form of *N. microps* occurring in the northeast Atlantic south of lat. 20°N. Adult males of *N. microps* without any photophore enlargement were also found in all oceans, but they occur mostly in the subtropical regions.

*Nematoscelis tenella* and *N. atlantica* males have two forms of photophore enlargement (Figure 11B,c and 11B,d): one form has the second and third photophores enlarged along with the presence of saddle-shaped paired plates on the dorsal side of both the first and second abdominal segments; the other form shows photophore enlargement on the fourth abdominal segment along with paired plates on the third abdominal segment. These two species occur together in the northern and southern subtropical provinces of all oceans. They also occur together in the tropical regions of the Atlantic Ocean. When the two species occur in the same geographical area, the males of both species do not show the same pattern of photophore enlargement. In such cases the pattern of photophore enlargement is as follows:

Species	Subtropics	Tropics
<i>Nematoscelis tenella</i>	First form*	Second form**
<i>Nematoscelis atlantica</i>	Second form**	First form*

\*Saddle-shaped plates on first and second abdominal segments and photophore enlargements on second and third.

\*\*Saddle-shaped plates on third abdominal segment and photophore enlargement on fourth.

*Nematoscelis atlantica* does not occur in the tropical regions of the Pacific and Indian oceans; *N. tenella* males in this region have the second form of photophore enlargement. There is no clear evidence of photophore enlargement in *N. difficilis* and *N. megalops*.

Even though a pattern of photophore enlargement appears to be characteristic of each species, not all mature males show this feature. When present, about 60-80% of the males in each sample had specific patterns of photophore enlargement as described above. Structure of the petasma of these forms did not differ from the typical forms. One is tempted to speculate on the evolutionary significance of this feature. The occurrence of the dorsal chitinous plate and the enlargement of the photophore in adult males may

have some joint functional importance, probably related to sexual behavior. Evidently, these abnormal conditions are not random phenomena; patterns are of specific nature and have clear association with sexual maturity. The fact that *N. tenella* and *N. atlantica* do not have the same form of photophore enlargement when they occur together in a geographical area suggests the possible role of these specific patterns in enhancing species recognition for mating.

## DISCUSSION

Among the morphological characters of a species, feeding and reproductive structures afford specific features that have diagnostic value. The specificity of the feeding appendages reflects presumed niche specializations. The structural uniqueness in the reproductive system ensures reproductive isolation of the species upon which the biological species concept is founded (Mayr 1942). Therefore, a key based on these characters should be the best in distinguishing individual species. The selection of the maxilliped as a diagnostic character has the advantage that the same key may be used for both sexes. However, it did not prove possible to make such a key for the larva.

The species of *Nematoscelis* can be grouped into two subgroups, one with *N. difficilis* and *N. megalops* and the other with the rest of the five species. The present study has brought out both ecological and systematic evidences to support such a grouping. The sequential development of larval characteristics also suggests phylogenetic differences between the two subgroups. Hansen (1912), using the structure of adult maxillule, proposed a division of *Nematoscelis* into these two groups. A similar division was also made by Mauchline (1967) on the basis of structural differences in the adult maxilla.

When closely related species are partially sympatric, behavioral mechanisms might operate to insure reproductive isolation of the species (Mayr 1966). Usually the presence or absence of intergradation between sympatric populations serve as indicators of interbreeding or reproductive isolation. Presumably, the absence of intergradation between species of *Nematoscelis* occupying the same geographical area suggests reproductive isolation. However, the absence of reproductive isolation between the two forms of *N. gracilis* is probably shown by the occurrence of sexually mature intermediate forms in the



overlapping regions of their distribution. The fact that the observed diagnostic feature lies on the reproductive structure would suggest probable genetic separation. Nonetheless, until more is known about the ecology and behavior of these forms, I do not wish to formally describe them as species or subspecies and will consider them ecophenotypes. The pattern of geographical distribution of these forms appears to be correlated with differences in environmental characteristics, particularly the distribution of dissolved oxygen in the water column (Gopalakrishnan 1974).

Allopatric populations are inferred to have undergone reproductive isolation if they are morphologically distinct and do not show any overlap in their diagnostic features. *Nematoscelis difficilis* and *N. megalops* are allopatric, occupying the northern and southern transitional zones of the Pacific respectively. *Nematoscelis megalops* also occurs in the Atlantic and Indian oceans. On the basis of similarities in the structure of the petasma of *N. difficilis* and *N. megalops*, Karedin (1971) questioned the validity of *N. difficilis*. Brinton (1962) considered them a sibling species pair evolved as a result of complete geographical separation. Although closely related, there are certain morphological features that distinguish one species from the other. Both quantitative and qualitative features of the reproductive system, the petasma in this case, indicate significant differences. The petasmae of *N. megalops* in the South Pacific, South and North Atlantic, and South Indian oceans show no apparent structural difference. These populations are probably in continuum facilitating gene exchange. (Communication between North and South Atlantic populations of *N. megalops* appears possible from the fact that only in this ocean does the characteristically subtropical species *N. atlantica* occur also in the tropics. This suggests that in the Atlantic the low-latitude boundaries of distribution of subtropical species approach the equator, permitting at least occasional north-south communication). The validity of *N. difficilis* can be supported by the fact that this species and *N. megalops* do not overlap geographically in the Pacific Ocean. Both species live in comparable environments (narrow mid-latitude zones) and therefore are probably exposed to similar selection pressures. In such a situation, even though geographical isolation would be complete, morphological differentiation might be slow. In the absence of gene exchange, the populations

would be expected to have diverged genetically. The relative lengths and shapes of the median lobe, proximal, terminal, and lateral spines of petasmae of the two species differ, supporting the validity of *N. difficilis*. In Hansen's words (1916) these differences are "certainly so sharp, so important, and so constant that they are sufficient for separating *N. difficilis* from *N. megalops*."

The *N. atlantica* population in the North Pacific is spatially separated from its counterpart in the South Pacific Ocean. No morphological distinctness was evident in this population, although it may prove to be genetically separate from others. *Nematoscelis lobata* is endemic to the Sulu and Celebes seas in the Indo-Australian Archipelago (Gopalakrishnan 1974). According to Hansen's (1916) description, this species is very similar to *N. microps*. The present study indicates that in many morphological characters *N. lobata* is more related to *N. atlantica* than to *N. microps*. *Nematoscelis lobata* and *N. atlantica* are allopatrically distributed and have probably acquired characters which promote or guarantee their reproductive isolation.

The observed differences in the structure of the first thoracic leg (maxilliped) of species of *Nematoscelis* indicate presumed specialization in feeding habits. All species of this genus are recognized to be omnivores. From a comparison of the first thoracic legs, it appears that species would be expected to show different types of feeding. *Nematoscelis microps*, *N. atlantica*, and *N. lobata*, having marginal setae (one row) on their propodus of the first thoracic legs, may be better fitted for filtering a large proportion of phytoplankton in their food, whereas *N. difficilis* and *N. megalops*, having three rows of setae on the propodus of the first leg, may select more animal food. In this respect *N. gracilis* and *N. tenella* are intermediate. Existing information on the gut contents of species of *Nematoscelis*, e.g., Nemoto (1967) and Weigmann (1970), is inadequate to substantiate this.

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